THE DEVELOPMENT OF ROOT HAIRS.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. LXXIV.

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(WITH PLATE I AND SIX FIGURES)

INTRODUCTION.

EXPERIMENTATION upon the effect of external agents on the development of root hairs is complicated by the fact that when external conditions are varied the internal factors are disturbed by an unknown amount. The varying of only one condition, which is the essential feature in accurate research, was thus extremely difficult, if not impossible. Therefore, the results to be set forth here are understood to be tentative. The last experimental work upon the immediate subject is that of SCHWARZ (**75**), to which the reader is referred for most of the earlier literature. Apart from three or four papers, the references to the causes for the development of root hairs are found incorporated, here and there, in reports on root studies, and as a rule are merely casual observations. The work here reported has been an endeavor to add some facts and suggestions as to the causes for the production of root hairs, variations in their structure not being considered.

LIGHT AND DARKNESS.

In view of the fact that in darkness there is generally an increase in the length of the axial organs and of their component cells (**47**, p. 64; **37**, p. 254), and because authors differ as to the effect of light and darkness upon the development of root hairs, it seemed best to reinvestigate the matter. SCHWARZ (**75**, p. 163) reports no effect; WENT'S (**85**, p. 8) experiments were not very convincing one way or another; DEVAUX (**10**, p. 306) finds that light retards growth and favors the development of root hairs; PETHYBRIDGE (**63a**, p. 235) reports that light retards the production of hairs upon the roots of oats and wheat growing in water cultures. The last experiment was repeated several times, but very little difference was noted

between the jars, the roots showing individual peculiarities of growth under both conditions. In one experiment the general growth in length seemed to be a little less in light, accompanied by a slight increase in the length and thickness of the hairs. In others no difference was noticed. No zonal arrangement was observed, as was mentioned by DEVAUX (**11**). According to MACDOUGAL (**47**, p. 246) the development of hair upon aerial organs in response to light conditions varies greatly, some plants having a tendency to decreased hair production in darkness, and others showing no change.[1]

A. Seedlings.

Preliminary experiments showed that the primary roots of seedlings of *Triticum vulgare*, *Zea Mais*, *Pisum sativum*, *Cucurbita Pepo*, *Vicia sativa*, *Helianthus annuus*, *Brassica alba*, and *Raphanus sativus* produced hairs, for a longer or shorter zone, in air or water regardless of the light conditions. This is attributed by SCHWARZ (**75**, p. 162) to the abundant food supply, seedlings being in a measure independent of external conditions for their existence.

Seeds of wheat, corn, pea, and squash were sprouted upon moist filter paper under illuminated and darkened bell-jars. On plants of the same age the hair zones were measured. No decided difference was found, though the hair zones averaged somewhat longer in darkness. The influence of the light was not strong and was probably indirect, through its effect upon growth.

An attempt was next made to compare the increase of surface per square millimeter under the two conditions. Seedlings of sunflower, white mustard, and radish were attached to pine bars by means of filter paper and rubber bands, as described by NEWCOMBE (**55**, p. 150), and placed in glass jars, one set being illuminated and the other darkened. The measurements were taken in all cases, as nearly as possible in the zone of best average development, near the top of the root. The closeness of the hairs varied in different parts of the root, but the average of the numerous counts was probably not far from fair. The increase (in square millimeters) per square

[1] In connection with the experiments here reported, the condition of the hairs on the epicotyl of etiolated and normal seedlings of Helianthus were compared. In the former case the cells were longer and the hairs were not only thus farther separated, but fewer cells produced hairs.

millimeter was calculated by multiplying the average length by the average width by the average number of hairs per square millimeter by π. Scrutiny of the results in the sunflower shows that for equally long roots the increase of surface varies, but that there is a slight predominance in the average increase of plants in dark (14.8) over those in light (14.02), and that this is entirely due to the greater average number of hairs per square millimeter (395 as against 373). The individual measurements for white mustard and radish show a like fluctuation of increase, but this time with a predominance in the average of light over darkness.[2] This is probably due to the fact that these are small seeds with little reserve food, and soon begin photosynthetic work in the light, while the plants in darkness have no such advantage. No evident difference in the length of hairs was observed in dark and light, as was noted by BENECKE (**5**, pp. 28, 29) for rhizoids of Lunularia.

B. Older roots.

Under ordinary conditions corn plants one or two weeks old, with roots growing through the bottom of the pots, did not produce hairs in water, whether illuminated or not. DEVAUX (**10**), on the other hand, found that light favored hair development on the roots of corn two months old growing in water. These plants, however, had been subjected to the rather severe operation of having all the roots cut off to one centimeter from the base, after which they were plunged into water. Upon repeating the experiment it was found that the plants in a day or so became yellow and unhealthy. In light five apparently healthy adventitious roots developed, and produced several isolated patches of hair, usually at the same time on all the roots, generally covered with a film of bacteria. In the darkened jar only three apparently healthy roots and two diseased ones were developed. No hairs or bacteria films appeared, although the odor of the culture betrayed greater decomposition than in the illuminated jar. Too many factors are involved to make the experiment, in its present form at least, of much value.

[2] Thus, mustard showed average increase, dark 41.33, light 44.11; and the radish, dark 29.44, light 32.09. Here also number of hairs, 321 to 344 and 345 to 357, accounts for the increase.

WENT (**85**, p, 8) found in aerial roots that light was not favorable to hair production except in very damp air, which makes it appear that with aerial roots in general moisture is of much more importance for hair development than light (PFEFFER **64**, p. 130).[3]

When seedlings of corn were allowed to send their roots through the bottom of the pots into moist chambers, one darkened and one left in diffuse daylight, little difference was observed between them, some roots in light producing more hairs and some less than those in darkness. There seemed a slight tendency for the hair to be thicker in light. MER (**51**, p. 584) found variation in the appearance of hairs on the different roots in the same culture, and considers "cette inégalité d'apparition des poils dans un même milieu est bien propre à montrer que leur développement est étroitement lié à la constitution particulière de chaque radicelle." No zonation such as DEVAUX (**11**) reports was noted in these cultures. In some cases, wheat, corn, and sunflower produced hairs in irregular zones, which however could not be traced to the effect of light and darkness. Any one of the many causes which may result in irregular growth might have been responsible. Where there is any effect on the development of root hairs produced by light, it appears from the above consideration to be due to the indirect effect upon growth. It does not appear to have the direct retarding influence as found by VÖCHTING in the case of the growth of willows and the development of new organs (**83**, pp. 152–162).

TEMPERATURE.

The effect of high and low temperatures upon growth has been studied by many investigators (**64**, pt. 2), with the general result that increase of temperature favors growth on account of greater or more rapid absorption. KIRCHNER (**29**, pp. 353–355) reports growth increased by high temperatures; NĚMEC (**54a**) found longer, thinner cells in warm water than in cold; POPOVICI (**67**, pp. 37, 88) states that high temperatures (33° C.) diminish the zone of elongation, while low temperatures, just above the germination minimum, increase it, although the total growth is less. KOSAROFF (**32a**)

3 For numerous instances of hair production on aerial roots touching a support, see the bibliography in WENT'S paper.

and KRABBE (**33**, p. 474) found roots to absorb less water at low temperatures. VAN RYSSELBERGHE (**70a**) considers that merely the rate of absorption is affected by the impermeability of the protoplasm. DEVAUX (**11**, p. 52) considers temperature to be of great importance in the production of root hairs, but has as yet merely made that preliminary statement. SCHWARZ (**75**, p. 158) reports that optimum temperatures (27–28° C.) do not overcome the inhibitory effect of water, as the roots grow smooth.

A comparison of the increase of surface in the cases of mustard and radish shows that temperature variations of small amount have no appreciable effect. The effect of greater changes was tested with seedlings of wheat and corn. These were placed in water at temperatures of 33–38° C. No hairs appeared on the parts in water, while the parts in air, as the height of the water varied a little, produced a few hairs.

Wheat seedlings in warm water, in water at room temperature, and in cold water, grew in all three conditions, and gave the following results:

Condition	Temperature	Duration	Result
Cold........	4.5–15.5° av. 11.6° (once 22.5)	Dec. 8–18	Haired to the tip, long and close set
Medium.....	16.0–29.5° av. 23.7°	Dec. 8–21	Hairs not so good, long bare spaces at tip
Warm.......	27.0–48.0° av. 34.5°	Dec. 8–14	Only two lived, smooth

Corn seedlings at temperatures of 29–37° (av. 33.4°) produced no hairs; while control plants at 16–27° (av. 22.9°) were haired at first, but later the root assumed its usual water type. This experiment was repeated many times with various modifications, and gave the same results.

That the smooth condition was due to the growth, rather than to the direct action of the heat upon the epidermal cells, was suggested by the following experiment. Corn seedlings were fastened in tap water of temperature 18–20° C., which was kept flowing in a very small stream from a rubber tube reaching the bottom of the jar. Under these conditions all the roots grew smooth and straight, omitting the seedling zone of hairs. Whether this was from the constant

supply of oxygen or on account of rheotropic stimulation by the rising water currents was not evident (*fig. 10*). The experiment was continued by varying the temperatures in the cold jar from 4–26°, giving very short hairs on one healthy root and on portions infested with bacteria. Once or twice a tuft of hairs was produced when seedlings were changed from cold to warm water, due possibly to retardation (ASKENASY **2,** p. 70; TRUE **80,** p. 400), but more probably to the more rapid adjustment and stretching of the epidermal cells in the warm water than of the inner cells. KIRCHNER (**29,** p. 353) found that 4° C. allowed of little or no growth of corn roots, while wheat elongated at 0°C., which may partially account for the different hair conditions in the two plants in cold water.

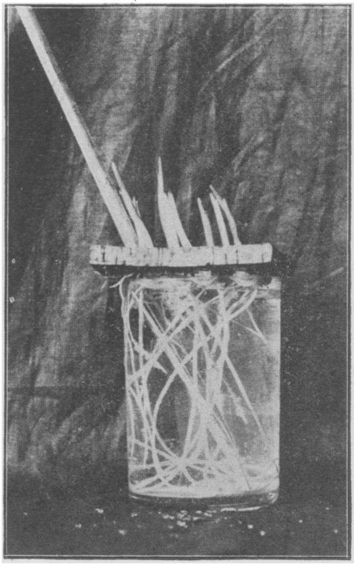


FIG. 10.—Corn roots growing in flowing tap water.

Wheat was planted in a pot of garden soil, and the roots allowed to come through the bottom and pass into warm water, of temperatures varying from 27–33° C. The roots were smooth at 33°, had scanty and irregular hairs at about 30°, and were more or less hairy at 27°. As this was tried repeatedly with the same result, it seems that for wheat, under these conditions, 30° C. is about the limit of hair production.

During a period of high temperature in the room, Elodea roots growing in soil were observed to be straight and smooth instead of kinky and hairy as is usual. When the temperature fell to the normal point, about 21° C., the roots assumed their usual aspect. In one case measured, the root growing in ground quartz at 27–34° C. elongated 4^{mm} in five days, and was curved and piliferous. The heat was not able under these conditions to suppress hair development. Another plant of Elodea growing in a glass cylinder had accumulated a little organic matter in the bottom of the vessel, not

enough to make a layer, and consequently not enough to offer any appreciable resistance to root growth. The roots growing along the bottom in this debris curled and developed hair in some places, but were smooth where they curved up into the water.

CONTACT.

Concerning the effect of contact upon the production of root hairs authors differ. SCHWARZ (**75**, p. 160) offers no explanation for their production in the case of water roots of Nuphar or Elodea entering the substratum, but thinks they are not due to contact, chemical stimulation, or retardation of the growth of the root. On air roots of aroids and orchids dry contact produced no hairs, nor was he able to cause them on Elodea (presumably in water) by contact with glass beads or ground glass. In air roots he speaks (p. 120) of the suppression of hair by too close contact. EWART (**14**, p. 237) makes the statement that "for the formation of root hairs on the root tendrils (of Vanila) moisture is essential, darkness and contact accelerating, and light and dryness retarding it." PFEFFER (**64**, p. 156) denies the effect of contact, attributing the hair development to greater moisture near the support. WENT (**85**, p. 8) also thinks that not contact but moisture and absence of light are the factors.

In the experiments here reported there was a production of hairs on the roots of Elodea not only when the root grew into the mud at the bottom of the aquarium, but also when ground quartz was substituted for the mud, while in every case roots growing freely in the water produced no hairs. Several of these straight, smooth roots were allowed to grow into ground quartz, and the tips were found usually much bent and curved, and in all cases covered with hairs. Sections were made from roots in water, soil, and quartz, and the cells were measured. The averages were:

MEDIUM	AV. LENGTH IN MM. OF CELLS		CONDITION
	Of epidermis	Of cortex	
Water..........	0.104	0.160	Smooth
Quartz..........	0.091	0.110	Hairy
Soil............	0.068	0.100	Longer hairs

There seems, therefore, to be a decided shortening of the cells in the substratum. As the mud at the bottom of the aquarium was of closer texture than the quartz, it probably offered greater resistance to the growth of the root. If the statement made by HABERLANDT (**22**, p. 188) concerning Elodea—"denen die Wurzelhaare in Wasser vollkommen fehlen, während sie beim Eindringen der Wurzeln in Erde sich reichlich einstellen"—means that the resistance of the substratum is instrumental in bringing about the production of root hairs, these results agree. The possibility of the chemical stimulus of the soil has been mentioned.

It does not seem probable that surface contact is a factor in the production of root hairs in soil, for when the earth is saturated the hairs on corn seedlings disappear, and those on wheat seedlings are decreased, although the soil particles are still there. This was stated by SCHWARZ (**75**, p. 160). In order to test the effect of contact with a smooth, solid body upon the epidermal cells of the root, corn seedlings were grown with their roots between glass plates, and in glass tubes open at the end. Where the roots filled the diameter of the tubes or the space between the plates, hairs were absent, both in air and water. On the sides not touching the plates hairs appeared nearly to the tip in air, and in the upper portions in water, as they do under ordinary conditions. Thus the contact on two sides of the root has no apparent effect on the hair production on the other two sides. Where the root did not fill the tube, hairs appeared in the usual zone in water and bent against the glass.

RETARDATION OF GROWTH.

It is of importance when speaking of the effect of growth upon the production of root hairs to indicate the effective stage. When the statement is made that slowing the growth of a root favors the production of root hairs (**51, 52, 11**), the retardation may be due either to fewer cell-divisions or to less elongation of the cells.

A. Rate of growth in air and water.

According to MER (**51, 52, 53**, p. 1279), retardation of the growth of a root produces or increases hair development. Thus lentil roots (**52**, pp. 665–6), growing straight and smooth in air, became piliferous when their growth was checked by the earth. Also, when

these roots and those of corn were papillate in air, passage into water checked their growth, caused curves, and made the hair longer at first, after which the roots grew smooth. Swellings and curves are generally covered with long hair, for which he offers the following explanation:

Lorsque les substances plastiques ne sont pas entièrement utilisées par l'extrémité végétative, ainsi que cela arrive quand l'accroissement de cette dernière est entravé par une cause quelconque, elles se portent sur les éléments voisins et principalement sur les cellules épidermiques dont les parois libres peuvent se développer plus facilement. De là des renflements, des radicelles et des poils.

SCHWARZ (**75**, p. 149) does not consider MER'S results trustworthy, and thinks that the checking of growth cannot cause development of hairs; but on the other hand that hair production goes with optimum growth energy (p. 155). MER repeated his experiments with the same results (**51**). SACHS (**71**, p. 410) found that the growth of roots in water is more rapid than in air. SCHWARZ (**75**, p. 154) reports slower growth in water than in air or earth, with a consequent decrease of hairs. Rapidity of growth caused by optimum temperature, however, was not able to overcome the inhibitory effect of water (p. 155). The following quotation is not quite in harmony with his criticism of the explanation offered by MER: "Am längsten werden die Wurzelhaare im feuchten Raume, und wenn das Wachsthum der Wurzel durch Nutation u. s. w. besondere Hemmung erleidet."

JAR I.

24-HR PERIODS	GROWTH IN 24 HRS. (mm.)		GROWTH PER HR. (mm.)		Temp.	CONDITION
	Water	Air	Water	Air		
I	32.0	..	1.33	....	..	
II	....	21	....	0.88	..	
III	14.0	..	0.58	....	12°	Hairs half way down
IV	....	5	....	0.20	11	One tuft
V	4.5	..	0.19	....	14	No hairs
VI	....	7	....	0.29	19	Hairs back to one tuft
VII	6.0	..	0.25	....	18	Doubtful hairs at top
VIII	15.0	..	0.65	....	18	Evident hairs at top
IX	30.0	..	1.25	....	12	No hairs
Average	16.9	11	0.71	0.46	..	

JAR 2.

24-HR. PERIODS	GROWTH IN 24 HRS. (mm.)		GROWTH PER HR. (mm.)		Temp.	CONDITION
	Water	Air	Water	Air		
I	15	..	0.63	....	12°	Few towards top
II	....	6	....	0.25	11	No hairs
III	7	..	0.29	....	14	No hairs
IV	....	10	....	0.42	19	Hairs back to last air period
V	15	..	0.63	....	18	No hairs
VI[4]	5	10	0.84	0.42	18	Abundant in air, none in water
VII	15	..	0.54	....	12	Little evidence at top
VIII[5]	....	10	....	0.42	18	Abundant
IX[5]	....	6	....	0.25	12	Good hairs
Average	12.5	8.4	0.52	0.35	..	

An attempt was made to ascertain whether the difference in rate of growth of corn seedlings in air and water could be the cause for the lack of root hairs in the latter medium. The seeds were planted in small pots in a mixture of sand and humus, or in garden soil, and the roots allowed to pass through the bottom of the pots. By placing the pots in the tops of wide-mouthed bottles half full of water, the roots hung in moist air, and by changing the level of the water, alternating conditions of air and water were brought about. The roots were allowed to remain in each medium for twenty-four hours.

It will be seen upon examination of the above tables that there was a general tendency to produce hairs in air and to cease their development in water. The effect of the air was not lost immediately, but in some cases the hairs extended a short distance into the water. I see no satisfactory explanation for the non-appearance of hairs in the first air measurement in *jar 2*. Lack of energy from low temperature appears to be the most simple explanation. The short growth in the following water period was still in the elongation phase when placed in air, and hairs are developed by differential elongation. Other experiments not recorded here gave the same general results.

4 Grew into water and the different rates could not be calculated; so that as two air periods of 10^{mm} growth had a rate of 0.42^{mm} per hr., that was assumed for this calculation.

5 Measurements of a root at the top of the jar.

Medium	Av. growth per day in mm.	Av. growth per hour in mm.	Av. length of cells in mm.	Approximate no. of cells per day
Air...........	8.6	0.36	0.067	128
Water........	11.2	0.45	0.085	132

The lengths of the cells are averages from measurements of air and water roots twenty-four hours old, having the same length as the average growth per day in the respective medium. We find that the rough approximation of the number of cells formed per day gives about the same result for the two media; consequently the difference in length of the roots and in the rate of growth is due to the greater stretching of the cells in the case of the water roots.

B. Retardation by mechanical means.

Concerning the effect of retarding growth by mechanical means, SCHWARZ (**75**, p. 159) thinks it is impossible to produce hairs in this manner. He was not able to cause them to develop by stopping the growth of the root by wire gratings, nor in general by narrow tubes. The fact that the wire might have had a toxic effect would discredit the former method of experimentation. He does not consider the resistance of the earth to be a cause for hair production (p. 160), but states that it results in developing hairs nearer the tip. While this may not be due to a greater number of cells producing hairs, it at least indicates the favoring effect of resistance, in that hairs elongate in a region which otherwise only shows the papillae.

A pot of corn was placed in the top of a glass cylinder, with the roots passing through the bottom and entering the water. One root grew horizontally and struck the side of the vessel, becoming kinked and hairy. On May 9 it was drawn away from the glass, and on the next day showed a smooth space. On May 12 the root again reached the glass, and on May 15 showed hairs. The jar was darkened and a glass rod was placed under a smooth vertical root, as in diagram, *fig. 11*. On May 14 the root showed hairs, but had swung free and was growing smooth. A plaster cap was unsuccessful, as it killed the tip of the root. With the death of the tip many laterals grew out producing hairs, some touching the glass and bending, and some becoming kinky in free water.

A second cylinder was set up as in *fig. 11*. The glass rod was

placed under a smooth straight root, but in twenty-four hours the root had curved and grown past the surface, a tuft of hairs on the curve indicating that some retardation of growth took place. For over a week the curling and hair production continued, then the root grew horizontally and struck the glass side. It became kinky and hairs continued to be formed for five days.

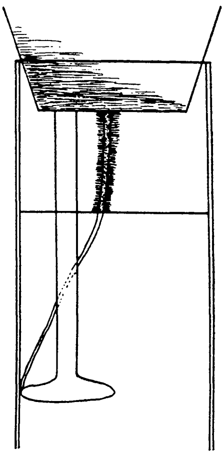


FIG. 11.—Diagram of apparatus to stop the growth of a root by a glass rod.

The fact that kinking takes place in free water shows that some other factor or factors besides resistance must be acting, but the facts brought out in the two experiments make it appear possible that resistance may be a partial cause for the kinking and hairiness of roots.

As the plaster cup in the preceding experiment was unsuccessful, glass tubes were tried. They were of sufficiently small bore to prevent a relief of pressure by too great bending. Smooth roots of corn were repeatedly allowed to grow into glass tubes (*fig. 12*). Usually the tip became more or less swollen, nearly or quite filling the tube. Primary roots showed kinking at the bottom, and hairs appeared in diminishing lengths from the bottom to the top. Only a few hairs appeared on the adventitious roots. When kept at high temperatures (24–34°C) the roots grew smooth, although bent and curved. If the resistance were relieved by allowing the roots to curve above the tube, hairs ceased to appear, conforming with the statement of MER (**51**, p. 584) that feeble retardation is not able to produce hairs. In one experiment the growth appeared to be so great that the roots were crushed and broken, producing no hairs on these portions.

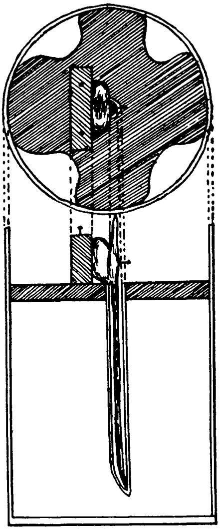


FIG. 12.—Diagram of apparatus to stop the growth of a root by a glass tube.

C. *Wounding.*

SCHWARZ (**75**, p. 158) was not able to cause hair formation by cutting off the roots 2–10^{mm} from the tip, nor by burning the tip with caustic. In my experiments the results were various according to the conditions. If the wound were not of sufficient depth to retard growth, if it were beyond the elongating zone, or if the plants were grown in warm water, no swelling or hairs appeared; otherwise hairs were produced. Thus in corn seedlings the tips of primary roots were pinched off about 1^{mm} from the tip. One showed hairs upon the swollen tips; another sent out a tuft of hairs and then grew smooth. In the latter case the wound was not of sufficient depth to more than slightly retard the growth. Of roots cut and burned, several showed hairs, the burned ones curving; several simply stopped growing and produced laterals; while others showed no effect. The cut tips of corn roots growing in air and producing short hairs became slightly swollen in twenty-four hours, and long hairs appeared above the cut. Both in light and darkness hairs were produced above the cut, whether the swelling appeared or not. This may have been due to the appearance of new hairs among the old ones, or to the stimulated growth of some of the old hairs, but more probably to the retardation of the zone in process of formation when the operation was performed. DEVAUX (**10**, p. 308) states that new hairs may appear among the old ones, but appearances which might be interpreted in that manner might be due to arrested development of some of the hairs. This would be difficult to decide, unless hairs were actually seen to originate between others (*fig. 2*). SCHWARZ (**75**, p. 165) and HABERLANDT (**75**, p. 187) state that hairs are always produced in acropetal succession.

D. *Medium.*

SACHS (**71**, p. 410) found that roots of land plants grew more rapidly in soil than in air or water, and his results have been confirmed by WACKER (**84**, pp. 109–115). The latter, however, found that in slimy soil the growth was retarded more than in water, and the denser the material the slower the growth. PFEFFER (**66**, p. 320) says the rate of growth is not affected by the density of the medium, roots growing as rapidly in fluid clay as in water. These conflicting

results are due probably to the different amounts of water in the soils used.

Roots of corn grown in ground quartz, garden soil, and air gave these results: in quartz, av. length 19.5^{mm}, hairs abundant; in soil, 22.3^{mm}, hairs good; in air, 50^{mm}, hairs poor. From these figures it seems that the resistance of the substratum bears direct relation to hair production; but the factor of water supply has undoubtedly an important influence, the quartz being less compact and therefore drier than the garden soil. Other experiments showed slower growth in air and quartz than in soil or water.

The behavior of roots of Elodea in the substratum has been mentioned, with the suggestion that retardation due to the soil particles was the principal factor. It will be shown later that a diminution of oxygen supply has a tendency to suppress hair production. There is less oxygen in the substratum than in the freely flowing water above it. It appears, therefore, that retardation, whether from soil resistance or chemical influence, must be the chief factor in producing the kinking and the hairs. Whether the hairs are due to the kinking, or both are due to the retardation of growth, cannot be stated. The production of hairs by retarding growth with glass tubes took place at times without kinking, though in the majority of cases the two results were associated. SCHWARZ (**75**, p. 159) considers "nutation" (kinking) the most potent factor in the production of root hairs, but it seems as if they might both be referred to unequal retardation of the growth of the root. Measurements of the epidermal cells of roots of Elodea give the following averages in millimeters:

Medium	Smooth	Haired
Water	0.104	.....
Quartz	0.110	0.077
Soil	0.128	0.065

Here the soil roots show better hairs than the quartz, and have the shortest cells when hairy. As will be seen later, however, the comparative lengths of cells of different roots can only be taken as supporting not as decisive evidence.

Corn seedlings were allowed to send their roots between glass

plates, on one of which was a layer of paraffin with sections covered with dune sand and ground quartz. The growth over the paraffin was smooth; the roots running over the sand were wavy, in some places producing hairs; and the one on the quartz kinked with more hairs (*fig. 13*). One root from the plant growing over quartz

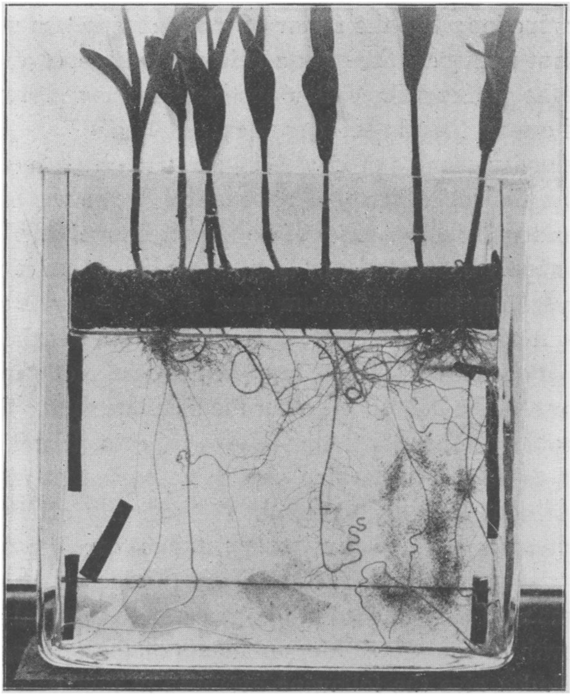


FIG. 13.—Corn seedlings growing in water in a glass jar between paraffined glass plates, on which was spread in the center a layer of coarse ground quartz; on the right is dune sand; on the left is clean paraffin.

wandered into the paraffin section, curled, and developed hairs. This appeared at the same time as the curling of the main root and may have been correlated with it. A second experiment with the sections horizontal also showed the laterals wavy at the same time that the main root kinked on the quartz.

WATER CONTENT.

According to several investigators (WIESNER **88,** p. 149; PFEFFER **64,** p. 100; PALLADIN **59,** p. 371; BRENNER **7,** p. 435; MACDOUGAL

47, p. 64; *et al.*) the attenuation of the axial members of etiolated plants, where it occurs, is due, in part at least, to a lack or diminution of transpiration. A greater proportion of water in etiolated plants is reported by MACDOUGAL (**47**, p. 64), PALLADIN (**60a**), JUMELLE (**28**, p. 386), *et al.*

Whether turgor is the cause or the result of growth, elongation of a cell is directly connected with its turgescence, greater water content producing greater elongation. Besides instances of etiolation, this is shown by the curling of roots which rest on the surface of water (SACHS **71**, pp. 398–9); by the rounding up of filamentous algae (LIVINGSTON **43**, p. 308; **44**, pp. 310–312) and of fungi (RACIBORSKI **68**, p. 111) upon withdrawal of water by osmotic solutions, and by the tendency of cells to stretch radially from loss of water by transpiration (KOHL **31a**, p. 297). The more turgid a cell becomes, therefore, the greater the tendency to stretch in a longitudinal direction. The water content of the root cells may be affected by changing the moisture content of the air, by altering the water content of the soil, or by surrounding them with solutions of higher osmotic pressure.

A. Transpiration.

It is well known that aerial transpiration favors the production of hairs upon aerial organs, WOLLNY (**89**, pp. 418–435) reporting an increased number of piliferous cells by count. On the other hand, some hairy-leaved plants grown in an aquatic habitat become smooth (COSTANTIN **8**, p. 40), and many have noted the absence of hairs on roots in water. Experiments to determine the effect of transpiration from leaves upon the development of root hairs gave negative results. Roots grown in saturated air at various temperatures showed few or no hairs, and any change that reduced the moisture content favored their development. Control plants showed that the temperatures used could not alone produce the results.

B. Saturated soil.

For these experiments corn and wheat were chosen because the former is very sensitive to the inhibitory effect of water, and wheat readily develops hair in that medium.

Corn roots grown in garden soil kept moist were found well covered with hair after seven days. Other pots were submerged in water for eight days. The uninjured primary roots showed long bare spaces and the laterals were nearly or entirely bare. One plant was allowed to dry out and the roots again became haired.

Wheat was grown in garden soil in pots, one of which was placed in water and the other watered a little every day. After a week's growth, the plants were found to have abundant hair on the roots passing through the pots into water, only zones of papillae on the roots in saturated soil, but good hairs on those in the dry pot. The zones may correspond to the drier conditions when the water fell below the bottom of the pot. In a control experiment precautions were taken to obviate the possible effects of a lack of mineral salts in the water on account of the absorptive action of the soil particles. It seems therefore that something besides lack of nutrient salts (probably lack of oxygen) must in this case be the important factor.

C. Osmotic solutions.

In connection with the experiments with osmotic solutions, cleaned sand was saturated with solutions of lactose, saccharose, and glucose of a concentration which allowed the zone of hairs to form. In lactose and glucose the hairs were much reduced and their presence in saccharose was extremely doubtful.

The effect of solutions upon the growth of plants and plant organs has been extensively investigated, but many of the results reported are of little use on account of a failure on the part of the investigators to distinguish the physical effect due to the osmotic action of the solution, and the chemical effect of the ions (LIVINGSTON **44**, pp. 124–7). Many authors (NOLL **57a**, GERNECK **18**, *et al.*) think the characteristics of water roots to be due to the lack of nitrates in the culture. The results of GERNECK and KRASSNOW (**36a**), showing that roots were richly haired in $CaNO_3$ solution, while the usual number of hairs or less were developed in KNO_3 solutions, make it appear that the kation has some special effect, and the mere absence of nitrates may not be the only factor to be considered in connection with the form and structure of water roots. Mere speculation on the subject, however, is of little value; careful physical

and chemical experimentation is necessary. SCHWARZ (**75**, pp. 156–7) reports a cessation of hair production in "concentrated" solutions (15 per cent. $CaCl_2$ and KNO_3 and 10 per cent. nutrient salts), but no distinction is made between the physical and chemical effects of the solutions. PETHYBRIDGE (**63a**, p. 235) found root hairs more or less variable in his cultures of inorganic salts.

The results of my experiments are too incomplete and inconclusive to warrant detailed publication. Many of the plants died, and often an experiment when repeated did not give exactly the same result as before. Some factor or factors seem to have escaped observation. A possible variable factor is suggested by the variable results obtained by BENECKE (**5**, p. 24) with Lunularia buds, when he used different kinds of glass for the vessels. Considering such sources of error my results could only be considered as suggestions for further investigation.

Among non-electrolytes, lactose, saccharose, glucose, glycerin, and mannite were used, in normal solutions (1 gram-molecule to 1 liter of water). Dilutions were made from this, sometimes with tap water boiled and cooled in the air and shaken to renew the oxygen content, sometimes with unboiled tap water, sometimes with distilled water, and sometimes with distilled water redistilled from glass. The most convenient method of experimentation proved to be to nearly fill stender dishes with the solutions and to float upon the surface of the liquid round cakes of paraffin about one-quarter of an inch thick with funnel-shaped holes in which the seeds were firmly wedged. This method avoids pins and the cakes in a measure protect the solution from bacteria. They were easily kept clean and could be remelted for each experiment.

In ten experiments with lactose (nine with sunflower and one with corn) five showed variable limits (0.2–0.4 N) for hair growth. In 0.5 N solution very little growth of the roots took place, and only once were papillae found under the microscope. The seedling zone of hairs grew best in water and diminished with increasing concentration.

In five experiments with saccharose two sunflowers gave 0.5 N, one 0.4 N, and one 0.2 N (with boiled tap water) as the limit for hairs; but the growth was not good. Allowing sunflower roots to

grow through pots into water and solutions made with tap water, the 0.5 N solution produced the best hairs. Corn roots growing through pots into water and solutions made with redistilled water showed hairs for the first three days; then they began to grow smooth, probably having become accustomed to the solution (WIELER **87** p. 376), as the strongest solution was the last one in which they became smooth. The pots were then transposed in various ways to test the effect of change. A transfer from a low concentration to a high one does not seem to be so favorable to hair production as the reverse. The roots seemed to be able to bear higher concentrations of saccharose than of lactose or glucose (cf. LIVINGSTON **44**, p. 295).

In three experiments with glucose in boiled tap water, sunflowers showed very poor growth, 0.5 N being about the growth limit and 0.1 N the limit for hairs.

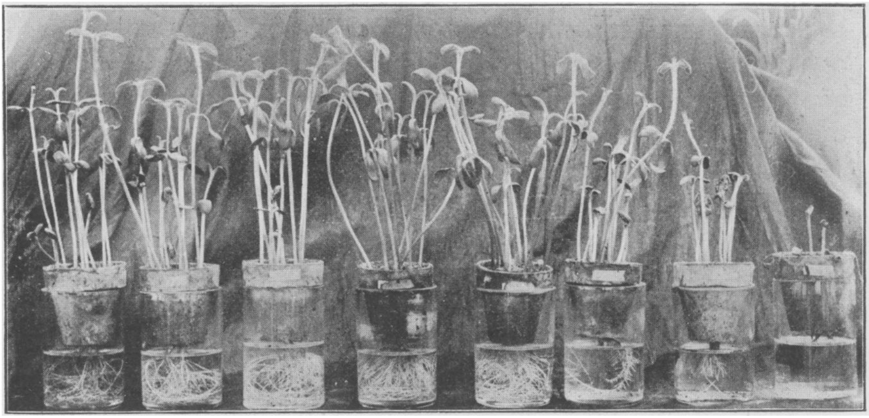
In two experiments with glycerin in boiled tap water with sunflowers, one showed hair limit in 0.05 N and the second in 0.2 N solution. In the latter case one jar had roots haired nearly to the tip.

In two experiments with mannite, sunflowers showed very poor growth, with 0.1 N limit for growth and hairs.

The only electrolytes used were the salts of Knop's solution, and potassium nitrate alone. The modified Knop's solution "D," used by LIVINGSTON (**43**, p. 299), was used for two experiments with sunflower seeds. The best hairs appeared in 0.2 N, where they grew to the ends of the roots. The limit for growth appeared to be 0.4 N and the limit for hairs 0.3 N solution. Sunflower roots passing through the bottoms of pots gave very good hairs in 0.1 N solution, but were not healthy in 0.3 N solution. The unmodified Knop's solution made up with redistilled water was used in various dilutions, 0.1 N being made with distilled and also with tap water, 0.2 N and 0.3 N with tap water, while cultures in redistilled water were used for control. After ten days all but 0.3 N showed some hairs, the best appearing in 0.2 N. The redistilled water gave the zone of hairs which appear in tap water.

In two sets of experiments with potassium nitrate, 0.016N solution gave the best hairs on corn roots. The roots were inclined to be knobby and swollen in the stronger solutions, and the 0.008 N acted

much as water did. *Vicia sativa* seemed more sensitive than corn, for in one set of experiments, performed at the same time as the above, 0.016 N solution killed the root tips and 0.008 N gave the best hairs. Sunflower roots allowed to grow through the bottoms of pots into water and various KNO_3 solutions made with tap water grew best (in average length of roots) in 0.05 N and 0.1 N, 0.4 N entirely stopping the growth of roots. Hairs appeared on all parts of the roots in 0.2 N solution, and more or less on the roots in all the solutions in which the roots grew (*fig. 14*).



H_2O 0.01 0.03 0.05 0.1 0.2 0 3 0.4

FIG. 14.—Seedlings of sunflower growing in a series of KNO_3 solutions.

The ill effects of distilled water on living protoplasm has been shown by LYON (**46**) and LOEB (**45**, p. 67). In my experiments with distilled water the behavior of roots was irregular; sometimes they would grow well, as in one case of Vicia and another of corn; in other cases the primary roots would not grow into it, for example wheat. As a rule, however, distilled water and water redistilled from glass gave less hair than tap water. In one or two experiments with wheat the tips of the roots stopped growing when they entered the water, and laterals were sent out (the longest nearest the tip) and produced some hairs. This peculiar branching was also observed in several cases of corn in distilled water and sunflower roots growing into KNO_3 solution, and even more markedly in the case of wheat

seedlings from which the seeds had been removed, and which were growing in water culture (*fig. 3*). In this last case the laterals were very long. It seems probable that in each of these instances we have to deal with a problem of nutrition, but how cutting off the supply of stored food can cause the tip to branch, as it does when the growth is checked, is not evident.

FOOD.

The possible effect of the quantity of food in the seed upon the development of the zone of hairs in water has been mentioned. SCHWARZ (**75**, p. 162) found that if the food were taken away (how he does not state) or used by acceleration of growth by heat, the hair production ceases sooner than usual, the length of the zone depending on the size of the seed. Several experiments were performed to test the effect of removing the food supply from seedlings. Seedlings of sunflower were cut off at different distances from the tips of the cotyledons and then placed on floating cakes of paraffin so that the radicles passed through into the water. Many died, but of the number which survived the best hairs grew on those with the longest cotyledons. According to TOWNSEND (**79**, p. 518) injury to one part of a plant causes disturbances in others, and the fact that the seeds were mutilated may have had a harmful effeet on the root; but from the whole set of experiments it seems fair to say that the greater the food supply the better the hair development.

Among the seeds which show the zone of hairs in water may be mentioned sunflower, corn, white lupine, pea, squash, etc. Others, as oats, wheat, mustard, etc., continue to produce hair in water until the food is exhausted and the plants die. In the case of the plants which form the zone, the cessation of hair production may be due to the hydrostatic pressure of the water; to lack of mineral salts, oxygen, or transpiration; or to the stimulating effect of the water upon growth of the root. Hydrostatic pressure can hardly be the cause when corn roots produced hair continuously in dilute solution of presumably the same pressure as tap water.

OXYGEN.

Although much has been written upon the relations of air and oxygen to growth, here as elsewhere little has been done upon root hairs. The statements of VÖCHTING, PERSECKE, and SCHWARZ seem

to be the only available information on the subject. PERSECKE (**62a,** p. 548) considered the development of root hairs to depend upon the amounts of air and water in the interstices of the soil. WIELER (**86,** pp. 223–4), SCHAIBLE (**74a**), *et al.*, report an increase in the growth of roots as a response to a decreased oxygen pressure. ARKER (**1a**) found that by passing air through water or soil, or by diminishing the air pressure above the soil or water, the roots grew faster. This he thinks was due not to the greater quantity of oxygen but to its greater mobility. The quantity of oxygen necessary for growth according to WIELER (**86,** pp. 213–4) is very small and varies with the plant. He found optimum pressure for *Vicia Faba* to be 5–6 per cent., for Helianthus 3 per cent., a retardation of growth taking place at 0.14–6 per cent. according to the to the plant. VÖCHTING (**82,** p. 94) found the roots of potato tubers to cease producing hair when the oxygen pressure fell to 3 per cent. The growth was slow, therefore the absence of hairs could not in this case be attributed to rapid growth of the roots. VÖCHTING also found (**83,** p. 132) in experimenting with willow twigs that there was sufficient oxygen in water to support life, but not enough for the production of new organs, a supply from above the surface being needed for the production of roots and shoots. WACKER (**84,** p. 110) considered that *Lupinus albus* and *Vicia Faba* died in saturated earth on account of the lack of oxgyen and the presence of harmful disintegration products, and believes land plants not to be able to supply oxygen to the roots by way of the aerial organs. SCHWARZ (**75,** p. 160) tried to overcome the inimical effects of water upon root hair production by passing oxygen through the culture fluid, but did not succeed in producing hairs, and came to the conclusion that other factors than lack of oxygen must be considered.

In the experiments here reported the oxygen content of the medium proves itself an important factor. Comparing corn and wheat in their ability to produce hair in water, we find that under apparently the same conditions the former grows smooth, while the latter produces long and abundant hairs. We may be dealing with the individual ability of the two plants to make use of the same amount of oxygen in a dissolved form, or with the individual needs of the plants for oxygen. Besides, one plant may be better able to supply its roots

with oxygen from the aerial parts than the other. Several experiments to show the effect of diminished oxygen pressure upon the production of root hairs gave similar results and only one need be reported.

A pot of corn, the roots passing through the bottom, was sealed into the top of a jar half full of a solution of pyrogallic acid. The surface of the soil was also covered and sealed with paraffin, leaving a very small hole for watering. Any oxygen entering this hole had to pass through the moist soil before it entered the jar, where it would be absorbed by the acid. In some cultures this hole was plugged up with paraffin without altering the results of the experiment. The oxygen pressure started at normal at the sealing and was gradually lowered to a possible zero. By twenty-four hours the roots were growing smooth, while those in the control jar showed good hairs. The growth was slow, consequently the lack of hair was not due to the rapidity of growth. Suppression of hair was the result when the CO_2 was also absorbed (by KOH), showing that the relative increase of that gas was not the cause of the cessation of hair production. Wheat roots proved to be very sensitive to the lack of oxygen. Several experiments set up as above, but substituting wheat for corn, did not give any result because the roots quickly turned brown and died. In one jar, however, several of the roots lived for a day, elongating in that time from 0 to 4^{mm}. These living roots showed no hair for some distance above the tips.

The experiment with corn was varied in the following manner, to see if the vapor of the pyrogallic acid had the effect upon the hairs. The pot was sealed in as before, the jar, however, being half full of water, boiled and cooled, covered to prevent as much as possible the absorption of oxygen. Air was forced through two jars of pyrogallic acid, finally passing through the water to wash it of any vapor. The apparatus was arranged as shown in *fig. 15*. The jar was measured previously and equal contents marked. The water at first was at *a*, and then the air was passed over slowly, displacing the water to *b*. If the air coming over were entirely free from oxygen, the per cent. in the jar would be half the normal amount. As the rate of passage would determine in great measure the completeness of the extraction of oxygen, an analysis of the oxygen content was not attempted, the aim being more to do away with the acid in the jar, and to get a less

complete extraction of oxygen than in former experiments, than to obtain quantitative results. The oxygen pressure was considered approximately one-half, and the roots indicated about the limit of hair production, showing irregular patches and scattered hairs with bare spaces. Repetition of the experiment showed the same condition of hair production. The temperature varied from 20–24°, which was probably not sufficiently high or low to effect hair production.

Willow twigs set up in Wolf's flasks in the same manner in about half oxygen content, with their lower ends in water, after three days showed hairs on the laterals in both jars. In seven days there was decidedly less air in the partial pressure jar. Left about two weeks longer, the hairs were better in both jars, appearing better in water than in air. This may be on account of accommodation to lack of oxygen (PFEFFER **64**, p. 2), or more probably to an increase in the supply by the green bark and the chlorophyll appearing in the roots.

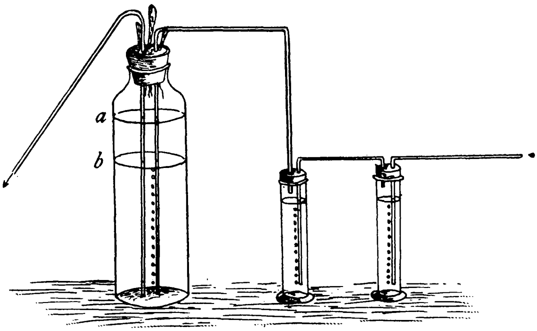


FIG. 15.—Diagram showing apparatus for diminished oxygen pressure; the air passes through two jars of pyrogallic acid solution before entering the experiment jar.

GENERAL CONSIDERATIONS.

Many writers (KRAEMER **34**; LEAVITT **40, 41**; VAN TIEGHEM **78**; JUEL **27a**; SAUVAGEAU **72**, p. 5 for Naias and possibly for other forms, **73**, p. 169) associate short cells with root hairs, in most of the cases mentioned the cells being preformed. From many measurements of sections cut from roots grown in these experiments there appeared to be a relation between the length of the cells and the growth of hairs, but there was no evidence of the preformation of the piliferous cells. No definite length of cell can be given as the limit for hair development, either in general or in a single species; the piliferous cells of one root may be longer than the smooth cells of another root of the same species. But an average derived from many

measurements of epidermal cells of roots grown under conditions producing hair is likely to be less than a similar average from the roots of the same species grown under conditions unfavorable for hair production. In the same root the average length of piliferous cells is less than that of smooth cells. SCHWARZ makes the significant statement (**75**, p. 177) that if in the roots of Elodea and Nuphar the short cells do not produce hairs, in time the difference in length is lost, thus indicating that the short cells stretch out if they do not grow into hairs. LEAVITT (**41**, p. 300) reports the same condition for *Nymphaea dentata*. In *Sagittaria Eatoni* (LEAVITT **41**, p. 292) and Phragmites (KRAEMER **34**, p. 22) the difference in size remains when no hairs are formed. The various statements concerning the condition of the root epidermis and the appearance of root hairs in the latter form are far from clear.

From *fig. 4* it will be seen that in corn root the origins of the hairs appear quite near the tip of the root, where the cells are isodiametric (OLIVIER **58**, p. 72). The statement that hairs appear in the zone where the cells have undergone considerable extension (LEAVITT **41**, p. 274) or are just ceasing to elongate (DEBARY **3**, p. 57) does not seem to be true generally. A probable explanation of the conditions observed by these authors is that the growth energy of the cell, after elongation has ceased, finds its expression in the rapid growth of the young papilla, which then takes on the typical appearance of a hair. By marking the roots of a series of corn seedlings growing in moist air, hairs visible to the eye were in several instances observed in the zone of elongation.

As mentioned above, in the plants studied there was no evidence of preformed piliferous cells; all the epidermal cells seemed capable of producing hair, and in corn at times did so. LEAVITT (**41**, p. 296) reports in some members of the Gramineae the whole epidermis to be piliferous. If each cell of the root epidermis is able to produce a hair, what prevents such an outgrowth from taking place? In water roots of corn we find the epidermal cells very much elongated and narrow. This characteristic extends inward through the cortex to the central cylinder, showing that the cells within as well as without are turgescent and stretching nearly equally. *Fig. 5* is a longitudinal section from a root of this water type. If, on the other hand, we

examine a root grown in air, we find the cells shorter and thicker, but not equally so, the outer ones, in all but a few cases to be considered later, being longer and thinner than those near the central cylinder, showing that the former are stretching more strongly than the latter. *Fig. 6* represents a section of such a root, grown in the same experiment as that from which *fig. 5* was taken. Tested with KNO_3 solution, the outer cells of an air root were plasmolyzed in 0.2 N, while the inner cells showed no shrinking, thus indicating that the latter had more concentrated cell-sap and less water. In water roots the epidermal cells were plasmolyzed in 0.2 N and the cortical cells shrank, but the protoplasm did not leave the walls. PFEFFER (**66,** p. 301) reports the turgor of the cortex cells of corn roots in air to be greater than that of the epidermis. In the air roots the epidermal cells seem to have more water, and to be able to stretch more than the inner ones. This can take place to a certain extent, but the inner cells cannot keep pace with them, but hold back the epidermal cells from their full elongation, and the growth energy finds an outlet in the direction of least resistance, *i. e.* the free outer wall. A similar occurrence is noted when Spirogyra is held in a plaster cast (PFEFFER **66,** pp. 240, 385), or when Stichococcus is made fast at the ends (KLERCKER **30,** pp. 94–5).

This bulging takes place in corn near the tip of the root, while the cells are isodiametric, and nearly the whole wall curves at first (*fig. 7*), but with the continued stretching of the cell this primary bulge becomes a papilla. The lagging behind of the inner cells of the cortex during the elongation period allows this papilla to become a hair. It seems then that hairs represent the ratio between the capacity of the epidermal cells to elongate and their ability to do so. If the capacity be the greater, the hairs will be produced; if equal to or less than the ability to elongate, no hairs will be developed. This would limit the statement of SCHWARZ (**75,** p. 155)—"bei dem Maximum der Wachsthumsgeschwindigkeit und unter den günstigsten Bedingungen bildet die Wurzel die zahlreichsten Haar"—to the epidermal cells.

Testing this explanation in the different cases reported here, I suppose first, in the corn roots growing with diminished oxygen supply, that the growth of the epidermal cells is decreased. The

inner cells on the other hand may obtain oxygen from the aerial parts, and thus with less moisture be able to keep pace with the epidermal cells growing with more moisture and less oxygen. In ordinary air the moisture and the oxygen reach the epidermal cells more abundantly than the inner ones, consequently the numerator of the fraction is increased as well as the denominator decreased, and hairs are developed. Upon the upper side of a corn root growing along the surface of water abundant hairs were developed, while the under side remained smooth. The difference in length between the epidermal cells and those of the cortex on the haired side was 20μ, and on the smooth side 6μ. KRAUS's tables (**37**, p. 254) dealing with the lengths of epidermal and cortical cells in relation to hair production are not very complete, and it seems useless to attempt to harmonize the results with those here reported.

KRABBE (**33**, p. 491) reports the inner cells of pith to be less turgescent than the outer ones when placed in water at 1–2°C, on account of the resistance to the passage of water offered by the protoplasts. According to VAN RYSSELBERGHE (**70**, p. 103) the influence of temperature is exhibited not in the total amount of water taken up, but in the rapidity of its passage. In warm water, therefore, the water reaches the inner cells and allows them to elongate sufficiently rapidly to keep pace with the epidermis, which is thus allowed to elongate to its full capacity and shows no hairs.

In the zone of hairs on seedlings in water cultures the available energy and the temporary retardation of growth (evidenced by the short outer and still shorter inner cells, and by the curling of many roots) combine to produce hairs. Also the presence of food may act as a stimulus to cause the cells to divide rapidly and form a thick root, whose inner cells do not get sufficient water, or oxygen, or both, to allow them to elongate as rapidly as the outer ones. Later, in the case of corn, the plumule elongates and probably supplies the inner cells with more oxygen. These are therefore better able to elongate, they are carried further from the food supply, division is less active, the roots grow more slender, the water supply of the inner cells increases, still greater elongation takes place, and the epidermal cells are allowed to stretch to their full capacity. Accommodation to a decrease of oxygen is mentioned by PFEFFER (**65**,

p. 70), and MER (**53**, p. 1279) speaks of the roots becoming accustomed to the medium.

The curving of corn roots in water is, according to Miss BENNETT (**6**) not aerotropic. BEAUVÉRIE (**4**) considers the turning up of water roots to be due to negative hydrotropism, for by using physiologically dry solutions he was able to get them to grow downward. In an experiment in which a slow stream of tap water was passed into the bottom of a vessel in which the roots of corn seedlings were growing, every one turned down, and grew straight and entirely smooth. The stimulus may have been a rheotropic one, or it may have been the presence of fresh aerated water which caused the omission of the hair zone.

An apparent exception to the explanation offered appeared in one root of sunflower grown in 0.5 N saccharose solution, in which the epidermal cells were shorter than the inner ones and still produced hair. Close to the tip, however, the papillae were found on cells shorter than the cortical cells, which makes it seem probable that the epidermal cells on the upper part of this root were shorter than the cortical cells from the start, as is the case with Elodea. In this plant the epidermal cells at the tip are very much shorter than those of the inner cortex, and the difference does not entirely disappear as the root grows older. Consequently there is not the same relation between the epidermal and cortical cells when hair is produced, as there is in corn. Measurements of the cells of roots of Elodea growing in soil, quartz, and water give the following averages in millimeters:

Medium	Cortex	Epidermis	Difference
Soil...........	0.100	0.068	0.032
Quartz........	0.110	0.077	0.033
Water.........	0.160	0.104	0.056

Upon examination of the table the greatest relative length of the inner cortical cells is seen to be in water, and the least in soil, with the hairs in inverse relation, as was the case with corn.

On the concave side of curved roots of corn the epidermal cells are shorter than the inner ones and at times show more hairs (*fig.*

8). Here the retarding action of the inner cells upon the epidermis is aided by the compression brought about by the curve. SACHS (**71**, p. 466) has shown that the average length of cells in a curve is less than in a straight portion of the root. MACDOUGAL (**49**, pp. 352–3) criticises SACHS' methods and reports the cells on both convex and concave sides longer than those on the same region of a normal straight root. His statement that the hairs are "abundant on the regions apical and basal to the region of greatest curvature, but are also wholly absent from the region exhibiting the shortest radius of curvature," seems to mean that the roots geotropically stimulated elongated at the curve and ceased to produce hair. In curving roots of corn growing in water, the epidermal cells appear to be restricted in their elongation, for curving almost invariably causes hair to develop. SCHWARZ noted this and called it "nutation" (**75**, p. 159). This term did not seem appropriate, and for want of a better word "kinking" has been used in this paper.

Transference from a solution of low osmotic pressure to one of high osmotic pressure appears to withdraw so much water from the epidermal cells that they do not grow into hairs. When the reverse order is followed there is a better chance for the epidermal cells to absorb water and to grow before the inner ones, and in this case some hairs appeared. The problem of the effect of osmotic solutions upon roots is quite different from that relating to filamentous algae and fungi. In the last two cases each cell is bathed in the solution to be tested, while with roots the action of the neighboring cells influences the epidermis, and on account of the thickness of the root the inner ones are not affected just as the outer ones. If a solution could be made which by its osmotic strength or chemical composition would retard the growth of the inner cells and allow the epidermal cells to grow, hairs might be expected. In one or two instances the epidermal cells of roots of sunflower and corn growing in 0.–0.2 N solutions seemed to become accustomed to the solution before the inner cells, and thus were able to grow out as hairs while the growth of the deeper cells was still retarded.

The retarding effect of diminished food supply on the production of hair on the internodes of the stem of potatoes is reported in a short note by KRAUS (**38**). In experiments with half seeds, one or two

cases occurred in which the central cylinder was torn apart at regular intervals by the stretching cortex, the epidermis bearing no hairs. The food supply seemed not enough to give the cells of the central cylinder sufficient strength to retard the stretching of the outer cells.

No change in turgor is needed to explain the appearance of root hairs, for according to PFEFFER (**64**[2], p. 29) there is no change when growth is accelerated by a rise of temperature or by absence of light, or when growth is retarded by lack of oxygen or (**66**, p. 296) by pressure. In the first three cases hairs disappeared or were diminished, while in the last they appeared.

An interesting relation was noticed between the epidermal and the hypodermal cells of some corn roots. In roots growing in the air and producing hair, the nuclei of the hypodermal cells were usually larger than those of the epidermal or cortical cells (*fig. 9*). This may indicate that the hypodermal cells were passing food to the outer cells, the starting of the lateral growth thus initiating a movement of material in that direction. SAUVAGEAU (**73**, p. 171) reports small hypodermal cells under the piliferous cells in Zostera. This demand for food by the outer layer would decrease the supply in the central cylinder and may account for the inverse relation between root hairs and lateral roots, noted by LESAGE (**42**, p. 110), COSTANTIN (**9**, p. 149), MER (**52**, p. 666; **53**, p. 1278), SACHS (**71**, p. 589), *et al.* In Eichhornia the lateral roots extend nearly to the tip, but there are no root hairs. This activity of the central cylinder, contrasted with that of the epidermis, is in harmony with the results of the experiments here reported.

In spite of the structural and functional similarity which often exists between root hairs and rhizoids, it does not seem appropriate to consider them together. In the first place, they are not morphologically similar, rhizoids being of gametophytic origin and root hairs developing from the sporophyte. The fact that rhizoids arise usually from a rather small gametophyte, all the cells of which retain in large measure their primitive condition, may account for the irritability they display toward geotropic, phototropic, and thigmotropic stimuli. Root hairs, on the other hand, are developed on a highly differentiated organ of a highly differentiated sporophyte, and are not thus sensitive, a difference pointed out by HABERLANDT (**22**, pp. 194–5).

It would be well to limit the term "root hair" to hairs borne by morphological roots only.

SUMMARY.

1. Light and darkness appeared to have only an indirect effect, through their influence on growth.

2. High temperature with sufficient moisture tended to decrease hair production by increasing the elongation of the internal cells.

3. The slower the growth in air the better the hair development.

4. Retardation of growth by glass tubes, by wounding, or by resistance of the substratum favored hair production.

5. Roots of seedling corn in water first curled and produced hair, possibly because of the retardation of growth by the diminution of oxygen or its presence in the dissolved state. Later the roots grew straight and smooth, either on account of accommodation to the oxygen supply or because the gas was supplied by the aerial parts.

6. Saturated air with high temperature tended to suppress hair development (*cf.* 2).

7. Saturated soil tended to suppress hair in corn and wheat, but other factors must be considered when Elodea develops hair in the substratum.

8. Osmotic solutions gave very irregular results on account of some undiscovered disturbing factor.

9. Less hair was developed in distilled water than in tap water.

10. Air deprived of oxygen stopped hair production and retarded growth.

11. Curves and swellings had a favorable effect upon hair development, probably because they represent the retardation of the growth of the root.

12. In all these examples of retardation favoring hair development, not the mere rate of growth, but the differential elongation of the inner and outer cells was of prime importance. Hair production depends on the ratio between the capacity of the epidermal cells to elongate and their ability to do so.

13. The activity of the epidermis may be in inverse proportion to the activity of the central cylinder, lateral roots often appearing when hairs are suppressed, and *vice versa*.

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EXPLANATION OF PLATE I.

FIG. 1. Longitudinal section of a corn root, grown in a glass tube: *a*, $\times 45$; *b*, two hair-producing cells lapping over the other epidermal cells, $\times 220$.

FIG. 2. *a*, Longitudinal section of a corn root, grown in air; the section shows more than one line of epidermal cells with long and short hairs; $\times 75$. *b*, rounded surface of a living root of corn, grown in redistilled water; the outlines of the epidermal cells were very indistinct; the only case observed where the difference in size was so great; $\times 45$.

FIG. 3. Roots of wheat plants which had been cut from the seeds shortly after sprouting; water culture; $\times \frac{1}{2}$.

FIG. 4. Longitudinal section of a root of corn, grown in air, showing the origin of hairs from the region where the cells are still short; $\times 220$.

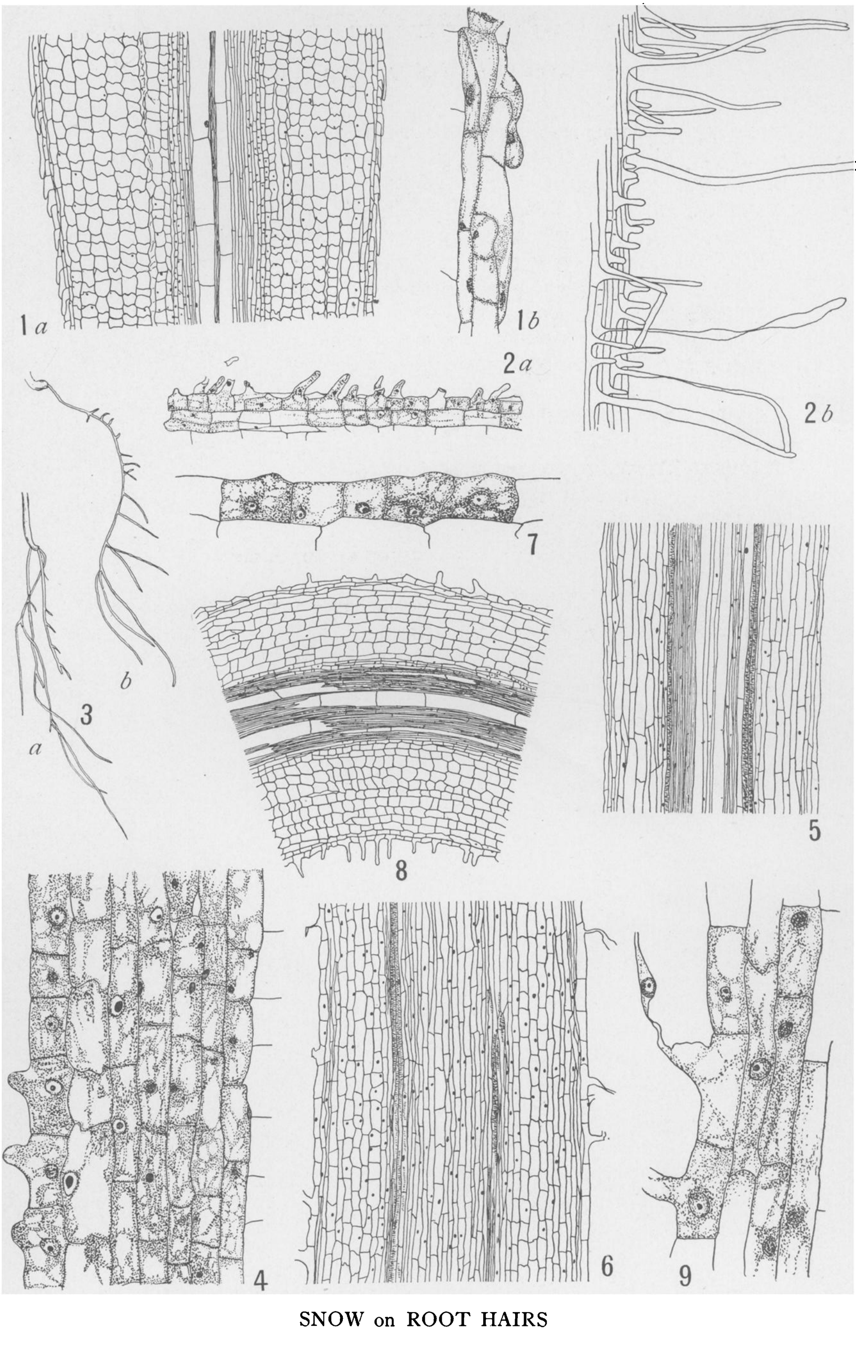
FIG. 5. Longitudinal section of a root of corn grown in water, in the same experiment with the root shown in *fig. 6*; $\times 45$.

FIG. 6. Longitudinal section of a root of corn grown in air, in the same experiment with the root shown in *fig. 5*; $\times 45$.

FIG. 7. Longitudinal section of a root of corn grown in air, showing the beginning of the hairs; $\times 220$.

FIG. 8. Longitudinal section of a corn root curving on the surface of water; $\times 34$.

FIG. 9. Longitudinal section of a corn root grown in air, showing one of the large nuclei of the hypodermal cells; $\times 220$.



SNOW on ROOT HAIRS